MALE FORETARSAL VARIATION IN LYCAENIDAE AND RIODINIDAE, AND THE SYSTEMATIC PLACEMENT OF *STYX INFERNALIS* (LEPIDOPTERA)

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Abstract.—I describe and illustrate male forelegs, particularly the tarsus, of Lycaenidae, Riodinidae, and *Styx infernalis,* and note seven characters: (1) whether the male foreleg is used for walking, (2) presence or absence of pretarsal claws, (3) number of tarsomeres, (4) distribution of scales on the tarsus, (5) whether scales lie flat on the tarsus, (6) presence or absence of tarsal spines (A-Type trichoid sensilla) and (7) distribution of B-Type trichoid sensilla on the tarsus when present. Previous descriptions of the male foretarsus and pretarsus of riodinids and *Styx* were inaccurate, including a reported pretarsal claw in *Styx.* Characters of the *Styx* male foreleg are either shared with riodinids or are unique. This conclusion supports Harvey's classification of *Styx* as a riodinid, and is inconsistent with Ehrlich's and Scott's phylogenies to the butterfly families.

Key Words: leg characters, butterfly classification, Lycaenidae, Riodinidae, *Styx*

Morphology of the male foretarsus and pretarsus in the butterfly, *Styx infernalis* Staudinger, has been disputed. Ehrlich (1958) distinguished the male foretarsus and pretarsus of *Styx* from those of Riodinidae. He reported that male *Styx,* a monobasic genus from the eastern Andes of Peru, has a segmented foretarsus whereas riodinids have a fused male foretarsus. He noted a pretarsal claw (and possibly a second one that had been broken in the one foreleg that he had available for study) in *Styx* but not in riodinids (with rare exceptions). Forbes (1960:138), on the other hand, stated, "It is said that the South American *Styx infernalis* has developed legs in both sexes; in fact . . . the true male . . . has the proper reduced legs" of a riodinid. Harvey (1987) partially resolved this controversy by reporting that male riodinids may have a segmented tarsus and that male *Styx* lacks pretarsal claws.

The systematic position of *Styx* has like-

wise engendered controversy. Ehrlich (1958) erected a monobasic subfamily for *Styx* of rank equal to the Riodinidae (his Riodininae) and Lycaenidae (his Lycaeninae) on the basis of differences in the male forelegs and some other characters. This classification has been followed by many subsequent authors (e.g. Common and Waterhouse 1982, Ackery 1984). Further, using some of Ehrlich's results, Scott (1985) proposed a cladogram in which *Styx* is the first taxon to split off from a lineage leading to the Lycaenidae and Riodinidae.

The classification and phylogenies of Ehrlich (1958) and Scott (1985) have been questioned. Harvey (1987) placed *Styx* in the Riodinidae on the basis of two shared, derived character states: female foretarsal trichoid sensilla clustered centrally, not laterally, and lack of apophyses posteriores on the female genitalia. I (Robbins 1988) reported that *Styx* and Riodinidae (with the

exception of the Old World genus *Laxita* Butler) are the only butterflies that share the loss of a cluster of trichoid sensilla on the dorsal posterior inner face of the male foreleg trochanter, which supports Harvey's placement of *Styx* in the Riodinidae. Scott and Wright (1988) placed *Styx* in the Riodinidae (their Riodininae) "for the moment." I (Robbins 1987b) reported that Scott (1985) did not analyze the distribution of male lycaenid and riodinid foretarsal character states parsimoniously, casting doubt on his phylogeny.

The purposes of this paper are (1) to describe and illustrate the male foretarsal morphology of the Lycaenidae (*sensu* Eliot 1973), Riodinidae (*sensu* Stichel 1910–1911), and *Styx*, (2) to resolve the differing results of Ehrlich, Forbes, and Harvey, (3) to detail the qualitative differences in male foreleg morphology of Riodinidae and Lycaenidae, and (4) to use this information to assess the classifications and phylogenies of Ehrlich, Scott, and Harvey.

The scanning electron microscope (SEM) provides an opportunity to study leg structures in a detail not available to many previous authors, and I have made extensive use of it. I describe morphology of the male lycaenid and riodinid foretarsi by citing previous results and adding my new findings. I then report the morphology of the male foretarsus of *S. infernalis*.

Materials and Methods

I used specimens in the collection of the National Museum of Natural History for study except for males of *Styx infernalis*. Gerardo Lamas (Lima, Peru) loaned me a male specimen with both forelegs intact, and Phil Ackery (British Museum of Natural History) sent me Ehrlich's dissection of a male with one unbroken foreleg.

I prepared forelegs for study by briefly wetting them in 80% ethanol, soaking them in 10% potassium hydroxide for 24–48 hours, and rinsing them in water or ethanol. In some cases, I removed some or all scales

using fine watchmaker forceps and a brush with stout bristles. Specimens for the SEM were soaked for 10 minutes in absolute ethanol before being mounted on stubs, which were coated with carbon and gold.

Male Foretarsus and Pretarsus

Lycaenidae (*sensu* Eliot 1973). — The lycaenid male foreleg is unique among the butterflies. With few exceptions (see below), it lacks pretarsal claws (Bates 1861) (Figs. 2, 3), and its tarsus is fused (Bates 1861) (Fig. 1), ends in a stubby (Fig. 2) or downcurved point (Clench 1955, Eliot 1973) (Fig. 3), and possesses A-Type and B-Type trichoid sensilla (terminology from Ma and Schoonhoven 1973). A number of authors (Sibatani 1974, Higgins 1975, Miller and Brown 1979) reported a single pretarsal claw, but I found no structure that fits Snodgrass's (1935) description of a pretarsal claw, and believe that these authors misconstrued the down-curved point at the tarsal tip reported by Clench and Eliot in some lycaenids (Fig. 3). Scales cover the dorsal and lateral surfaces of the lycaenid male foretarsus, but not the distal ventral surface, where many trichoid sensilla occur (Fig. 4). Further, scales lie relatively flat on the tarsus surface so that B-Type trichoid sensilla are not covered by scales (Fig. 5). Lycaenid forelegs are used for walking (Bates 1861, Ford 1945) although a number of popular books mistakenly state the opposite (Howe 1975, Pyle 1981). Scales usually have longitudinal ridges with shingled and distally tapered scutes (Downey and Allyn 1975) (Fig. 6). These structures are not reported in trichoid sensilla, and in lieu of better evidence, I use them to distinguish scales from trichoid sensilla. I describe below the A-Type and B-Type trichoid sensilla on lycaenid male forelegs as well as distinctive setae that also may be trichoid sensilla.

(1) A-Type trichoid sensilla (spines). — Spines are stout trichoid sensilla, sometimes called "bristles," that have fluted sides and occur primarily on the ventral surface
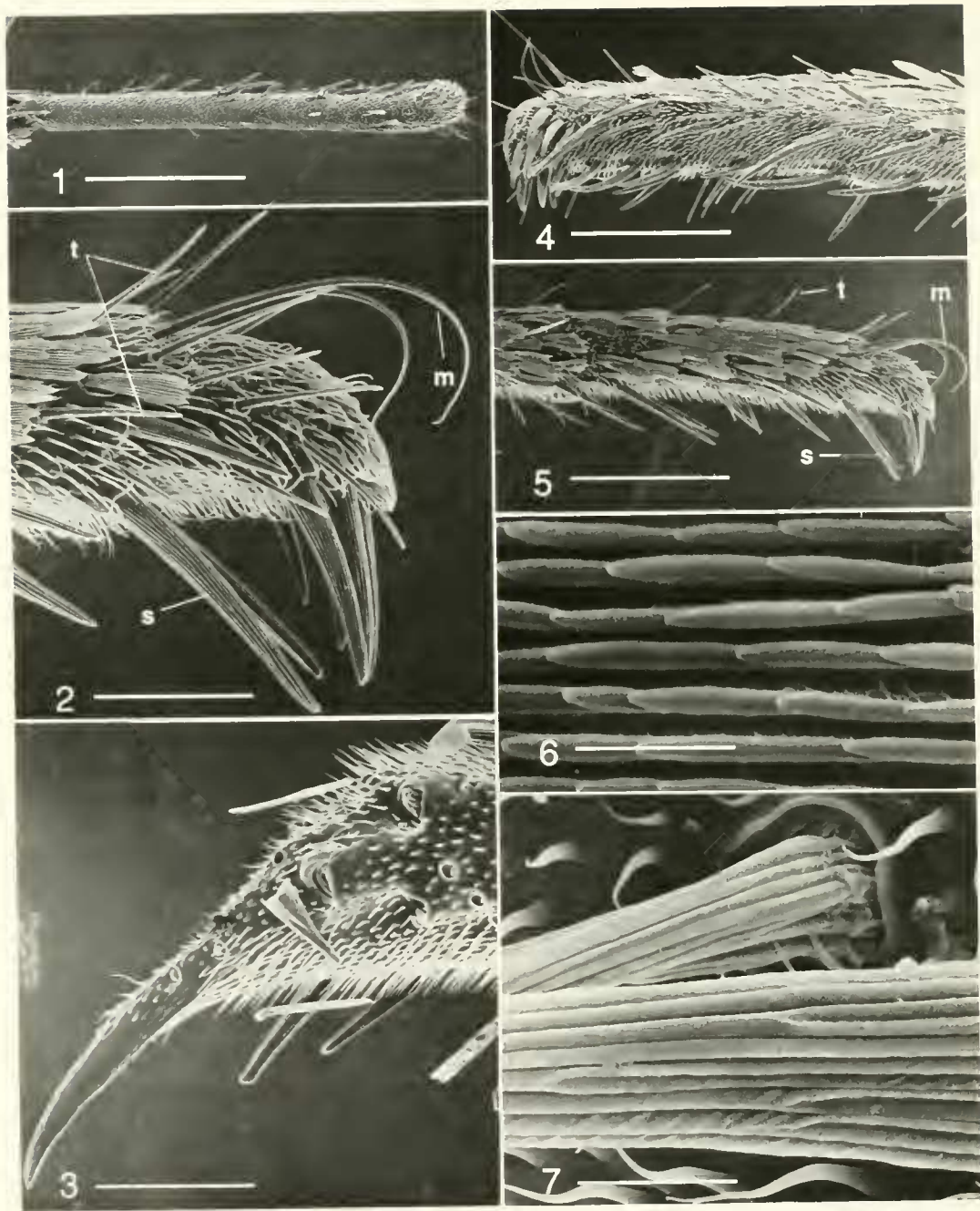
Figs. 1–7. Male lycaenid foretarsus. 1. "*Theritas*" *augustinula* Strand, dorsum, scales removed to show lack of segmentation. Scale line 600 microns. 2. *Calycopis cecrops* Fabricius, lateral view, stubby tip, spine (A-Type trichoid sensillum, labelled s), "macrotrichion" (m), B-Type trichoid sensilla (t), and lack of pretarsal claws. Scale line 60 microns. 3. *Lycaena editha* Mead, lateral view, down-curved point at tip. Scale line 75 microns. 4. "*Theritas*" *theocritus* Fabricius, ventro-lateral aspect, no scales on ventral surface, empty sockets of removed scales on lateral surface. Scale line 200 microns. 5. *C. cecrops*, lateral view, spine (A-Type trichoid sensillum, s), "macrotrichion" (m), and B-Type trichoid sensillum (t), which extends beyond scales that lie flat on the tarsus. Scale line 176 microns. 6. "*T.*" *theocritus*, scale showing scutes of longitudinal ridges, base of scale to right. Scale line 3 microns. 7. "*T.*" *Theocritus*, fine structure spines. Scale line 12 microns.

of the lycaenid foretarsus (Bates 1861) (Figs. 1–5, 7, 8) and other legs. Histology of spines in nymphalids (Eltringham 1933) and neurophysiology from nymphalids and pierids indicate that they are mechanoreceptors (Morita et al. 1957, Ma and Schoonhoven 1973). Those on female butterfly foretarsi are associated with clustered B-Type trichoid sensilla, and are apparently used to abrade leaves (reviewed in Chew and Robbins 1984), but may also be mechanoreceptors. Superficially similar spines occur on the ventral abdomen of some lycaenids and riodinids (Clench 1955, Inoue and Kawazoe 1966, Eliot 1973, Harvey 1987) and on butterfly antennae (Myers 1968, Grula and Taylor 1980), where they are presumed to be mechanoreceptors (Odendaal et al. 1985). Spines on legs and antennae always seem to occur in association with B-Type trichoid sensilla, as they do on the venter of the female abdomen in the lycaenid, *Curetis* Hübner (Robbins unpubl.).

(2) B-Type trichoid sensilla. — These sensilla are scattered over the dorsal, lateral, and ventral sides of the lycaenid male foretarsus (Figs. 1, 2, 4, 5). At magnifications below about 1000 times, B-Type trichoid sensilla on male lycaenid foretarsi appear to be smooth-walled (Robbins 1987a) (Fig. 2), but at magnifications above about 8000 times, they have a variable fine structure (Figs. 13, 14). It is unclear in the absence of histological and neurophysiological data whether there is one kind of B-Type trichoid sensillum on male lycaenid foretarsi with variable surface structure or if there are several morphologically and functionally different types. Another fine structure, in which there are ringed indentations (Fig. 15), occurs on female lycaenid foretarsi, but I have not found them on male lycaenid foretarsi. Undoubtedly, histological and neurophysiological techniques will be needed to establish homologies.

B-Type trichoid sensilla on butterfly legs are chemosensory and mechanosensory. Lycaenids extend their proboscis when their tarsi are exposed to water or sugar water (Anderson 1932), and Hodgson (1958) showed that trichoid sensilla respond neurophysiologically to sodium chloride, sucrose, and tactile stimulation. It has not been specifically demonstrated, however, that the B-Type trichoid sensilla on the lycaenid male foreleg are chemosensory, although this is a reasonable inference. Similar sensitivity among B-Type trichoid sensilla to water, sugars, sodium chloride, and tactile stimulation has been shown for a variety of butterflies (reviewed in Fox 1967), and Eltringham (1933) presented a histological description of these sensilla. Ma and Schoonhoven (1973) described the histology of a clustered B-Type sensillum on the female pierid foretarsus, and demonstrated that these clusters are sensitive to plant secondary compounds, water, sodium chloride, and tactile stimulation.

(3) "Macrotrichia." — Clench (1955) noted that a pair of long setae, which he termed "macrotrichia," occurs on the dorsal surface of the male lycaenid foretarsus just basal to the tip (Figs. 2, 5). Their surface structure at higher magnifications is distinctive (Figs. 9, 10), and these markings are often more pronounced towards their distal end. Whether these setae are scales or sensilla is currently unknown. Superficially similar structures are found in most other butterflies, even male Ithomiinae (Nymphalidae) that have the tibia and tarsus fused into a short segment (Fig. 11). In *Phoebis* Hübner (Pieridae), the analagous structures have scale-like longitudinal ridges and scutes (Fig. 12), similar to some piliform scales (Brown & Miller 1983). Kuznetsov (1967) illustrated similar structures in a sphingid and arctiid, termed them "setae" or "ungal bristles," and reported that their number varies in Lepidoptera from 2–10 and is "of definite taxonomic importance."

Some male lycaenids have a five-segmented foretarsus and pretarsal claws, which apparently have evolved at least four times in the Theclinae and perhaps once in the
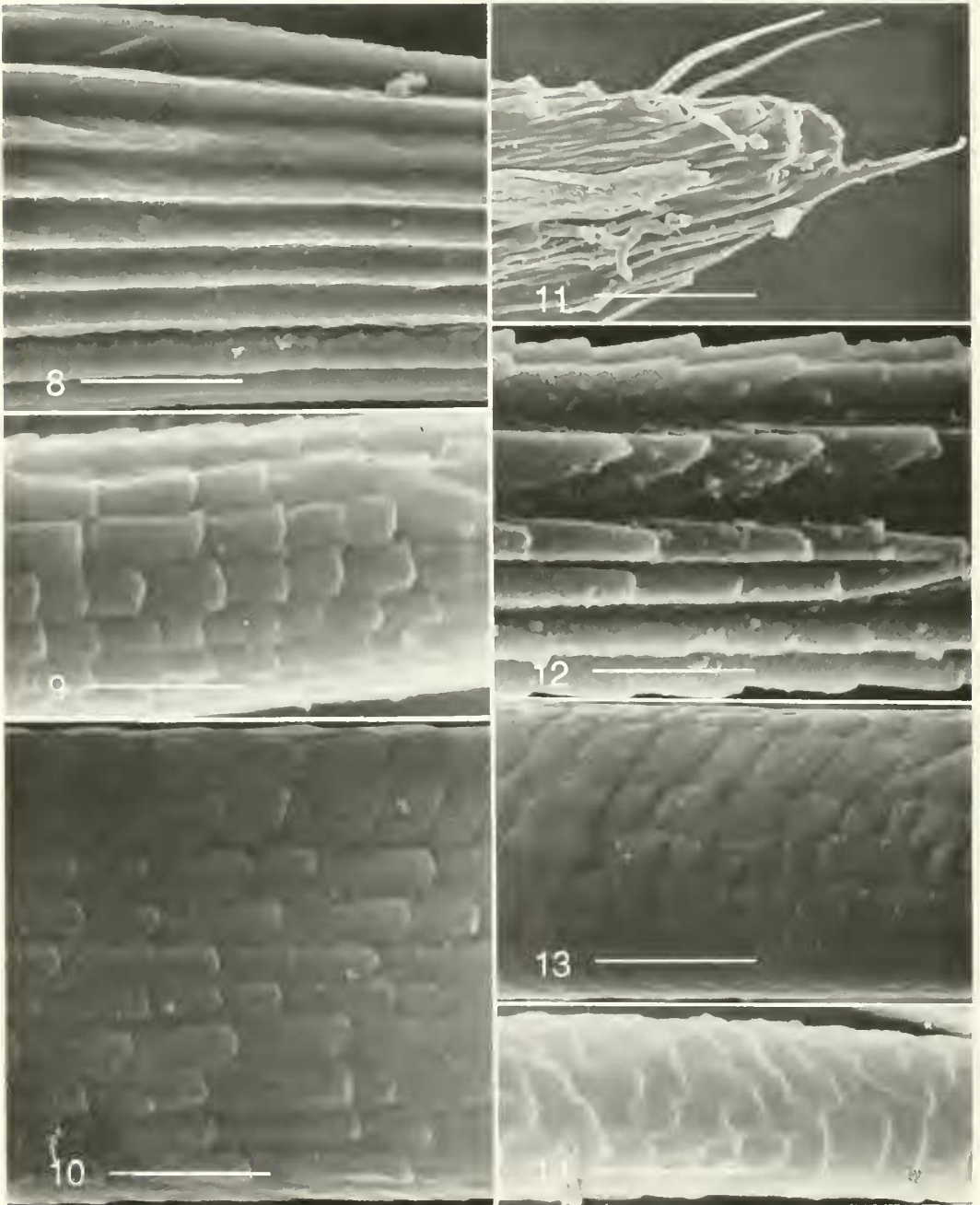
Figs. 8–14. Male foretarsi. Socketed base of sensillum to left in figures of their fine structure. 8. *Atlides halesus* Cramer (Lycaenidae), fine structure spine (A-Type trichoid sensillum). Scale line 6 microns. 9. *C. cecrops* (Lycaenidae), fine structure "macrotrichion." Scale line 2 microns. 10. *A. halesus* (Lycaenidae), fine structure "macrotrichion." Scale line 2 microns. 11. *Pagyris cymothoe* Hewitson (Nymphalidae: Ithomiinae), apex of fused foretarsus and tibia with "macrotrichia." Scale line 33 microns. 12. *Phoebis sennae* Linnaeus (Pieridae), fine structure "macrotrichion." Scale line 2.5 microns. 13. *A. halesus* (Lycaenidae), surface structure B-Type trichoid sensillum. Scale line 2 microns. 14. *C. cecrops* (Lycaenidae), surface structure B-Type trichoid sensillum. Scale line 2 microns.

Liphyrinae + Miletinae (Eliot 1973). Eliot (1973) suggested that if the "genes" for a segmented foretarsus and clawed pretarsus were on the Y chromosome, then crossing over with the X chromosome might account for its repeated evolution in males. However, the segmented male foretarsus lacks the clusters of B-Type trichoid sensilla found on female foretarsi, at least in *Theclopsis* Godman and Salvin (Figs. 16, 17), casting some doubt on this hypothesis.

Riodinidae (*sensu* Stichel 1910-1911).— Unlike the male lycaenid foretarsus, the male riodinid foretarsus is not used for walking (Bates 1861, Ford 1945), and is covered dorsally, laterally, and ventrally with elongate scales (the so-called "brush foot") (Figs. 18–21). It has from 1 to 4 tarsomeres (Godman and Salvin 1879–1886, Scott 1985) (Figs. 18–21), contrary to Ehrlich's findings, but segment partitions are sometimes incomplete (Godman and Salvin 1879–1886, Powell 1975), making a count of the number of tarsomeres somewhat arbitrary. The male riodinid pretarsus is like that of lycaenids in that it lacks claws (Figs. 18–21). Godman and Salvin (1879–1886) reported male pretarsal claws in *Apodemia nais* Edwards, but the three specimens that I examined lacked them. I have not seen any riodinid with male foreleg pretarsal claws, but remnant ones may occur in some species.

The occurrence of spines (A-Type trichoid sensilla) on male foretarsi differs between lycaenids and riodinids. Male riodinids lack foreleg spines (Bates 1861) (Figs. 18–20) although I examined one male of *Emesis* with a spine on one foretibia and none on the other. A striking exception is males of *Sarota* Westwood (Harvey 1987), which have many foretarsal spines (Figs. 21, 22).

The distribution of B-Type trichoid sensilla differs markedly between lycaenid and riodinid male foretarsi. B-Type trichoid sensilla are absent from the male riodinid foretarsus except at the distal end of the tarsus where "macrotrichia" also occur. These sensilla are difficult to discern be-cause they do not extend beyond the scales covering the tarsus as they do in lycaenids. I usually find one or two "macrotrichia" at the tarsal tip (Figs. 23, 25–27), and some-times a few B-Type trichoid sensilla (Figs. 23, 24). Many setae on the tarsus resemble B-Type trichoid sensilla at lower magnifi-cations, but at higher magnifications appear to be scales with longitudinal ridges and scutes (Fig. 28). It is not known whether the B-Type trichoid sensilla on the riodinid foretarsus are neurophysiologically active.

All riodinid male foretarsi may have B-Type trichoid sensilla and "macrotrich-ia" at the tip even though I could not find them in all preparations. Some scales have to be removed to see them, and in these cases, I may have removed them with the scales. However, the restricted occurrence of B-Type trichoid sensilla on the distal tar-sus where they are intermixed with elongate scales, whether or not these sensilla are pres-ent in all riodinid species, is quite different from their distribution in lycaenids, as de-scribed above. Further, even though male *Sarota* have spines similar to lycaenids, their B-Type trichoid sensilla are distributed ac-cording to the riodinid pattern (Figs. 22–24).

Styx infernalis.— The structure of the male *S. infernalis* foretarsus and pretarsus is sim-ilar to those of riodinids in some respects, and is unique in others. The *Styx* male fore-leg pretarsus lacks claws (Harvey 1987) (Figs. 29, 30), and in that respect, is the same as riodinids and most lycaenids. There is a lightly sclerotized structure at the tip of the tarsus that may be a remnant of the pretar-sus (Figs. 29, 30), perhaps homologous with the arolium. No riodinids have such a struc-ture. The distal edge of the lightly sclero-tized structure at the tip of the tarsus ap-pears dark under a light microscope, and may account for Ehrlich's report of a single pretarsal claw.

The male riodinid foretarsus segmenta-tion is unusual. One specimen (the Ehrlich dissection) has two tarsomeres with an in-dication of two other partitions while the
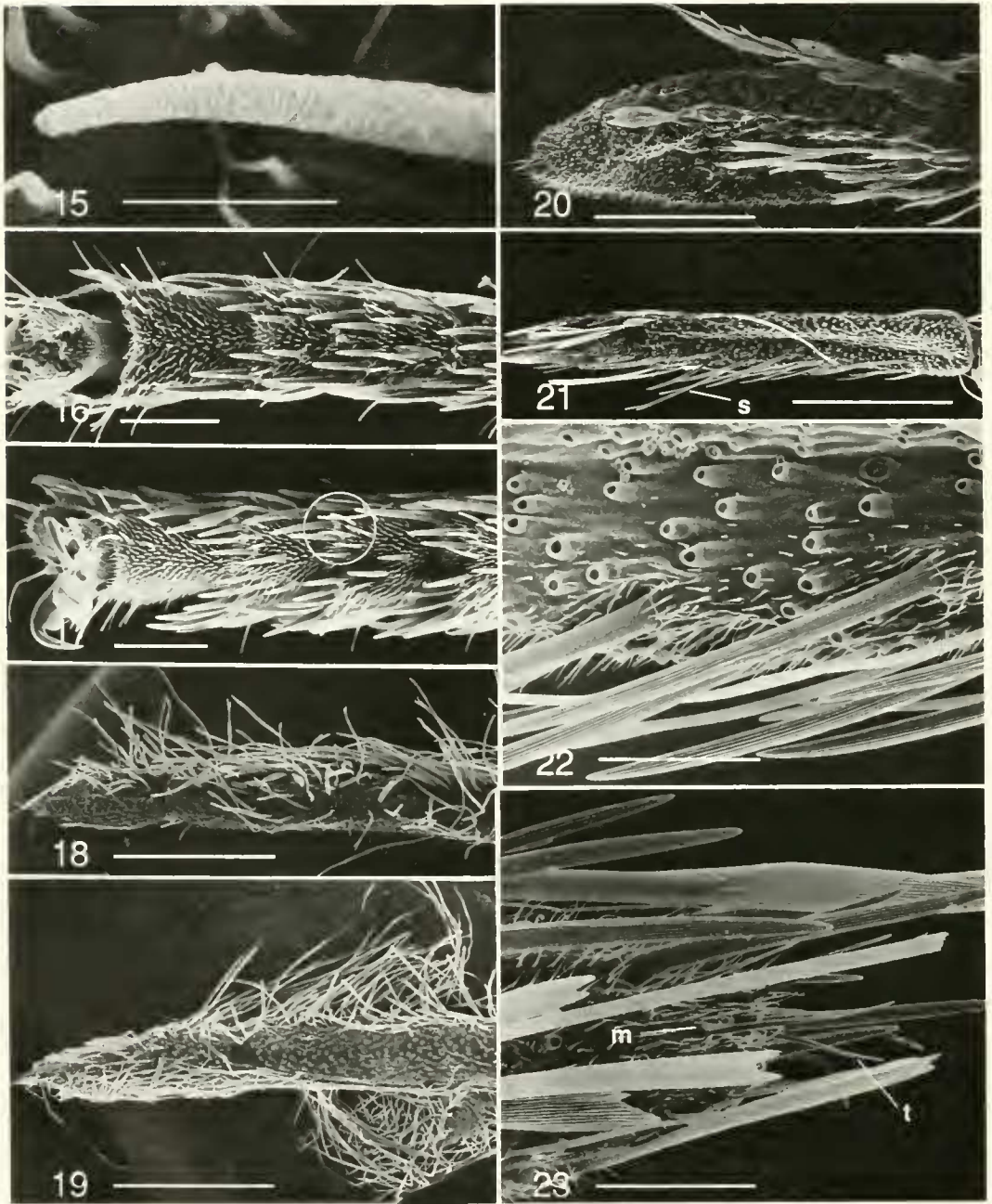
Figs. 15–23.   Foretarsi. 15. female *Liptena libyassa* Hewitson (Lycaenidae), fine structure clustered B-Type trichoid sensillum. Scale line 10 microns. 16. male *Theclopsis murex* Druce (Lycaenidae), ventral aspect, segmented, but no clustered B-Type trichoid sensilla. Scale line 100 microns. 17. female *T. murex* Druce (Lycaenidae), ventral aspect with lateral cluster of B-Type trichoid sensilla (circled). Scale line 100 microns. 18. male *Melanis pixe* Boisduval (Riodinidae), lateral aspect with most elongate scales on lateral and ventral surfaces removed (sockets visible), four tarsomeres. Scale line 380 microns. 19. male *Emesis mandana* Cramer (Riodinidae), lateral view with most elongate scales on lateral surface removed (sockets visible), three tarsomeres. Scale line 430 microns. 20. male *Stalachtis magdalenae* Westwood (Riodinidae), lateral aspect with most elongate

second specimen has four complete tarsomeres on both forelegs (Figs. 31, 32). Powell (1975) reported similar intraspecific variation in the number of tarsomeres in the male foretarsus of the riodinid *A. nais*. Segmentation in *Styx* appears to be more complete and to allow more intersegmental movement than in riodinids, but like riodinids and lycaenids, it has less than 5 tarsomeres.

The distribution of setae on the male foretarsus of *S. infernalis* is similar to that of riodinids. It has a sparse covering of elongate scales on all sides (Figs. 31, 32) with two "macrotrichia" on the dorsal end of the tarsus (Figs. 31, 32). One foreleg had no spines (A-Type trichoid sensilla) on the tarsus (Fig. 31), whereas the other foreleg from the same specimen had a spine on the second tarsomere (Fig. 33). B-Type trichoid sensilla occur on the last tarsomere, primarily on the ventral surface (Figs. 34, 35) except that one leg had one trichoid sensillum on the third tarsomere. The fine structure of these trichoid sensilla is superficially more similar to that of "macrotrichia" (Fig. 36) than to that of lycaenid and riodinid B-Type trichoid sensilla.

It is not known whether male *S. infernalis* use their forelegs for walking. Ehrlich (1958) noted that its male foretarsus is less than half the size of the pterothoracic legs and is doubtfully functional. Because other butterflies with "brush feet" do not use their forelegs for walking, I agree that the same is probably true for *Styx*.

DISCUSSION

The male foreleg of Lycaenidae differs from that of Riodinidae in a number of characters. (1) The foreleg is used for walking in lycaenids, but not in riodinids. (2) The distal, ventral surface of the tarsus lacks scales in lycaenids but not in riodinids. (3) Scales lie flat on the tarsus in lycaenids but not in riodinids. (4) The tarsus is wholly fused in lycaenids (with some five-segmented exceptions) whereas it is partially or wholly fused in riodinids with 1–4 tarsomeres. (5) The lycaenid tarsus possesses spines (A-Type trichoid sensilla) over much of the ventral surface whereas the riodinid tarsus does not, with the notable exception of *Sarota*. (6) The lycaenid tarsus has scattered B-Type trichoid sensilla that protrude beyond the scales while the riodinid tarsus has B-Type trichoid sensilla restricted to the tip where they are intermixed with elongate scales. (7) The foreleg is more than half the length of the pterothoracic legs in lycaenids and less than half this length in riodinids (Ehrlich 1958). (8) The coxa does not extend beyond its articulation with the trochanter, or if it does, it is arched upwards in lycaenids whereas it extends beyond the trochanter in a blunt process without being arched upwards in riodinids (Robbins 1988). (9) The trochanter has a cluster of small trichoid sensilla on its anterior inner surface whereas this cluster is lacking in riodinids (Robbins 1988).

The male foreleg of *Styx* is structurally that of a riodinid. It shares the riodinid character state for each of the 9 characters above except that data for the first character are lacking. Ehrlich (1958) was mistaken in finding similarity between the male foreleg of *Styx* and that of male lycaenids with a five-segmented foretarsus and clawed pretarsus.

The *Styx* male foreleg differs from that of riodinids in several characters. (1) The lightly sclerotized structure at the tarsus tip is

scales removed (sockets visible) to show lack of segmentation. Scale line 200 microns. 21. male *Sarota dematria* Westwood (Riodinidae), lateral view with most elongate scales removed (sockets visible), spine (A-Type trichoid sensillum, s) on ventral surface. Scale line 430 microns. 22. male *S. dematria* (Riodinidae), detail of ventral surface showing spines with fluted walls. Scale line 60 microns. 23. male *S. dematria* (Riodinidae), tip showing position of "macrotrichion" (m) and B-Type trichoid sensillum (t). Scale line 60 microns.
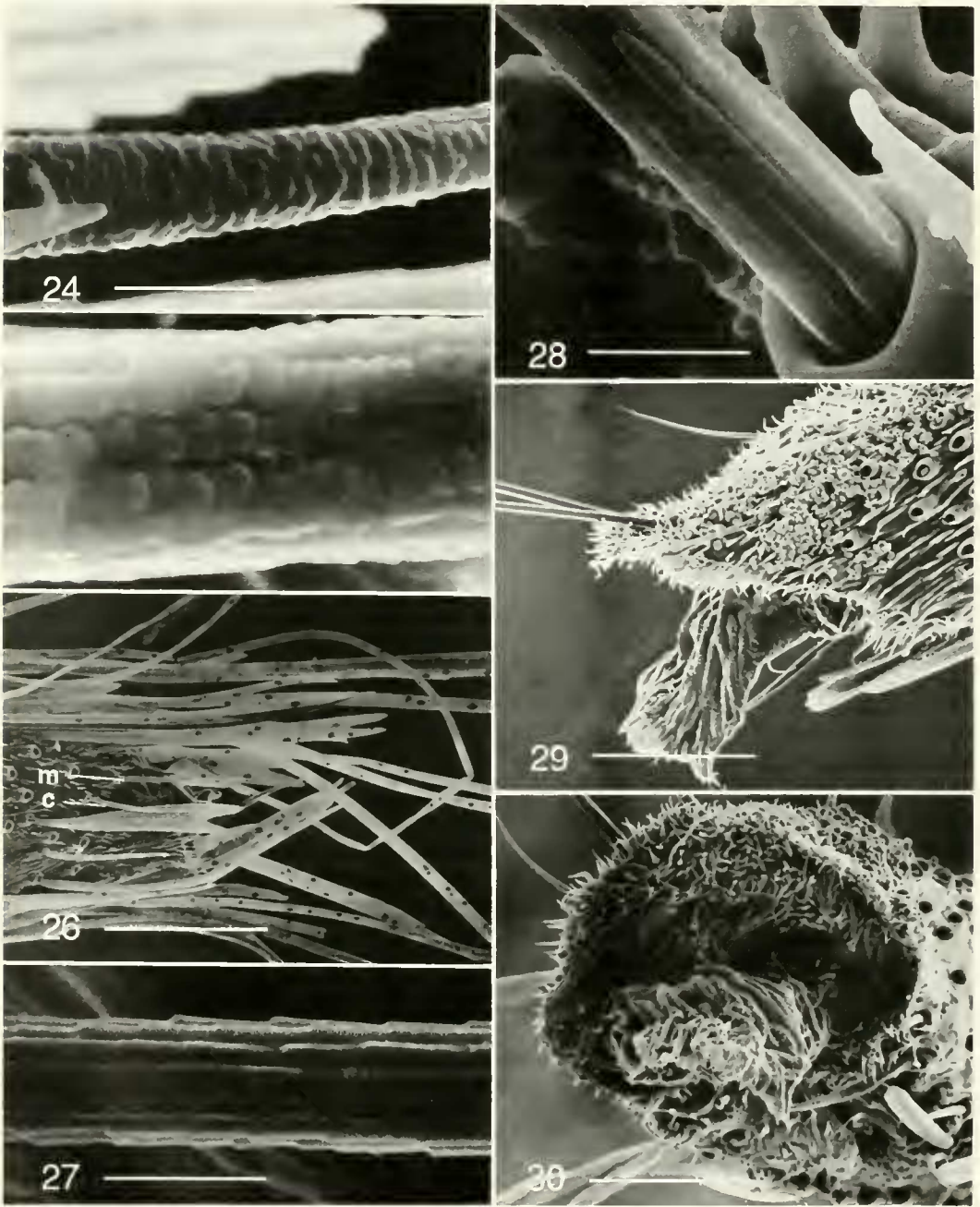
Figs. 24–30.   Male foretarsi. 24. *Sarota dematria* (Riodinidae), fine structure B-Type trichoid sensillum at apex. Scale line 3 microns. 25. *S. dematria* (Riodinidae), fine structure "macrotrichion" at apex. Scale line 2 microns. 26. *Hades noctula* Staudinger (Riodinidae), apex showing position of "macrotrichion" (m) and piliform scale (c). Scale line 87 microns. 27. *H. noctula* (Riodinidae), fine structure "macrotrichion" at apex. Scale line 2.5 microns. 28. *M. pixe* (Riodinidae), fine structure piliform scale at apex. Scale line 3 microns. 29. *Styx infernalis*, lateral aspect, lightly sclerotized structure at tip, no pretarsal claws. Scale line 60 microns. 30. *S. infernalis*, posterior aspect of 29. Scale line 50 microns.
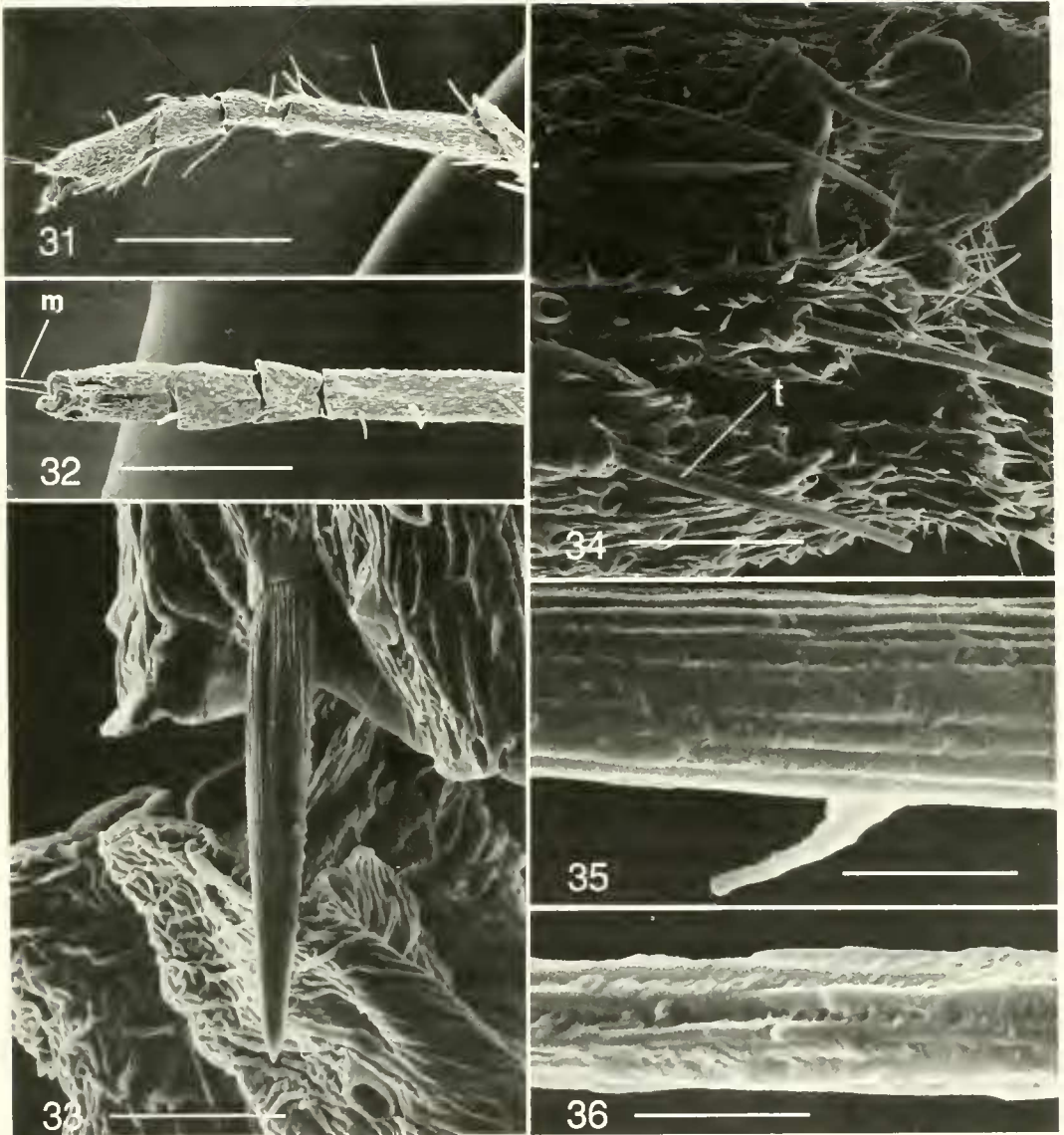
Figs. 31–36.   Male foretarsus of *Styx infernalis.* 31. Lateral view, four tarsomeres, "macrotrichia." Scale line 400 microns. 32. Ventral view, four tarsomeres, "macrotrichion" (m). Scale line 380 microns. 33. Spine (A-Type trichoid sensillum) on ventral surface of second tarsomere. Scale line 20 microns. 34. B-Type trichoid sensillum (t) on ventral surface last tarsomere. Scale line 38 microns. 35. Fine structure B-Type trichoid sensillum on ventral surface of last tarsomere. Note longitudinal lines instead of broken latitudinal lines in Lycaenidae and Riodinidae. Scale line 2.5 microns. 36. Fine structure "macrotrichion" dorsal surface of last tarsomere. Scale line 2.5 microns.

unique to *Styx.* (2) The tarsomere partitions in *Styx* appear to allow greater interseg-mental movement. (3) The forecoxa ex-tends a shorter distance beyond the tro-chanter in *Styx* than in most riodinids (Robbins 1988). (4) The trochanter of *Styx* lacks a cluster of trichoid sensilla on the dorsal, outer posterior surface whereas it is

present in riodinids (Robbins 1988). These four differences show that Forbes's description of the male *Styx* foreleg as typically riodinid was partially incorrect.

SYSTEMATIC POSITION OF *STYX*

Ehrlich (1958) placed *Styx* in its own subfamily (Styginae) of rank equal to the Riodinidae (his Riodininae) and Lycaenidae (his Lycaeninae). His evidence was (1) the occurrence of two recurrent veins in the forewing cell, (2) the form of the labial sclerite, (3) a strongly convex mesothoracic anepisternum, and (4) the morphology of the male foreleg. Ehrlich remarked that the first two character states are unique to *Styx* and the third is also "unique but close to the riodinines." These unique character states by themselves provide no evidence on the systematic placement of *Styx*. Either they evolved on the lineage leading to *Styx* only or they are part of a transformation series for which information from other characters is necessary to show the order of transformation.

Ehrlich noted that the male foreleg of *Styx* is close to lycaenids whose males have a five-segmented foretarsus with pretarsal claws. This comparison was incorrect because *Styx* lacks pretarsal claws and has less than five tarsomeres. Further, lycaenids, whose males possess a five-segmented tarsus and clawed pretarsus, have the lycaenid pattern of scales, spines, and B-Type trichoid sensilla (Fig. 16), not the one shared by riodinids and *Styx*. Thus, Ehrlich's evidence did not justify giving the Styginae rank equal to the Lycaenidae and Riodinidae.

Scott (1985) proposed that *Styx* branched from the lineage that then evolved into the Lycaenidae and Riodinidae. His evidence is that *Styx* possesses (1) a large anepisternum that became "slightly smaller" in the remainder of the lineage, and (2) eyes that are not notched at the antennae whereas the remainder of the lycaenids and riodinids have notched eyes.

While Ehrlich noted that the shape of the mesothoracic anepisternum is unique to *Styx* (but close to the riodinids), Scott considered its size to be a "primitive" character state, but did not indicate his evidence for this hypothesis. He did not measure the anepisternum nor indicate whether its size is allometrically correlated with body size. Further, the mesothoracic anepisternum is not a separate sclerite in Libytheidae and Pieridae, and is present in only some species of Papilionidae and Nymphalidae (Ehrlich 1958). Since this sclerite may be present or absent in potential outgroups and its size unmeasured when present, there is no evidence that a large anepisternum is "primitive" on the lineage leading to the Lycaenidae and Riodinidae.

Scott's statement that the Lycaenidae and Riodinidae (exclusive of *Styx*) have eyes notched at the antennae is inaccurate. Although it is true for many Lycaenidae and Riodinidae, some (*Hades* Westwood, *Euselasia* Hübner) have the same arrangement of compound eyes and antennae as *Styx*. In short, Scott provides no evidence for his systematic placement of *Styx*.

Harvey (1987) put *Styx* in the Riodinidae. He characterized the Riodinidae as those butterflies (1) with B-Type trichoid sensilla on the female foretarsus clustered centrally and (2) lacking apophyses posteriores on the female genitalia. *Styx* and riodinids (with the exception of *Laxita*) also share the loss of a trichoid sensillum cluster, which is present in all other butterfly families, on the male foretrochanter (Robbins 1988).

My results in this paper are consistent with Harvey's placement of *Styx* in the Riodinidae. The differences between *Styx* and other riodinids in male foretarsus structure are character states that are unique to *Styx* (such as the slightly sclerotized structure at the tip of the tarsus) and that provide no evidence on its systematic position. On the other hand, riodinids and *Styx* share 8

character states of the male forelegs. These results are consistent with Harvey's classification of *Styx* as a riodinid.

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